

General Mechanisms for Inverted Biomass Pyramids in Ecosystems

Hao Wang^{a,*}, Wendy Morrison^b, Abhinav Singh^c,

Howard (Howie) Weiss^a

^a*School of Mathematics, Georgia Institute of Technology, Atlanta, GA 30332, USA*

^b*School of Biology, Georgia Institute of Technology, Atlanta, GA 30332, USA*

^c*School of Physics, Georgia Institute of Technology, Atlanta, GA 30332, USA*

Abstract

Although the existence of robust inverted biomass pyramids seem paradoxical, they have been observed in planktonic communities, and more recently, in pristine coral reefs. Understanding the underlying mechanisms which produce inverted biomass pyramids provides new ecological insights, and for coral reefs, may help mitigate or restore damaged reefs. We present three classes of predator-prey models which elucidate mechanisms that generate robust inverted biomass pyramids. The first class of models exploits well-mixing of predators and prey, the second class has a refuge (with explicit size) for the prey to hide, and the third class incorporates the immigration of prey. Our models indicate that inverted biomass pyramids occur when the prey growth rate, prey carrying capacity, biomass conversion efficiency, the predator life span, or the immigration rate of prey fish is sufficiently large. In the second class, we discuss three hypotheses on how refuge size can impact the amount of prey available to predators. By explicitly incorporating a refuge size, these can more realistically model predator-prey interactions than refuge models with implicit

refuge size.

Key words: inverted biomass pyramids, coral reef, predator-prey model, refuge, immigration.

1 Introduction

The biomass structure is a fundamental characteristic of ecosystems (Odum, 1971). The shape of biomass pyramids encodes not only the structure of communities, but also integrates functional characteristics of communities, such as patterns of energy flow, transfer efficiency, and turnover of different components of the food web (Odum, 1971; Reichle, 1981; Del Giorgia et al., 1999).

A trophic pyramid is a graphical representation showing the energy or biomass at each trophic level in a closed ecosystem. Energy pyramids illustrate the production or turnover of biomass and the energy flow through the food chain, while biomass pyramids illustrate the biomass or abundance of organisms at each trophic level. When energy is transferred to the next higher trophic level, typically only 10% is used to build new biomass (Pauly and Christensen, 1995) and the remainder is consumed by metabolic processes. Hence, in a closed ecosystem, each trophic level of the energy pyramid is roughly 10% smaller than the level below it, and thus inverted *energy* pyramids cannot exist.

A standard biomass pyramid is found in terrestrial ecosystems such as grassland ecosystems or forest ecosystems, where a larger biomass of producers sup-

* Corresponding author: Telephone: 1-404-894-3949; Fax: 1-404-894-4409;

Email address: wanghao@math.gatech.edu.

port a smaller biomass of consumers (Dash, 2001). Although they appear to be rare, inverted biomass pyramids exist in nature. They have been observed in planktonic ecosystems (Del Giorgia et al., 1999), where phytoplankton maintain a high production rate and are consumed by longer lived zooplankton and fish. Recently, inverted biomass pyramids have also been observed in pristine coral reefs in the Southern Line Islands and Northwest Hawaiian Islands (Friedlander and Martini, 2002; Sandin et al., 2008), where the benthic coral cover provides refuge for prey fish (Figure 1). At least one prominent researcher suspects that an apparent inverted biomass pyramid exists on a reef off the North Carolina coast, and he speculates this is due to significant immigration of prey fish into the reef (M. Hay, pers. comm., 2008). In this manuscript, we introduce three classes of predator-prey models to study how inverted biomass pyramids can arise via these three distinct mechanisms.

2 Well-Mixed Mechanism

Most predator-prey models implicitly assume that predators and prey are well mixed, and many incorporate a Holling-type predation response (Holling, 1959a,b). Although the “well mixed” assumption is usually far from being satisfied when prey are animals, it appears to be a reasonable assumption for phytoplankton-herbivore interactions in aquatic ecosystems, and we first discuss the existence of inverted biomass pyramids in this setting.

We begin by considering the standard Lotka-Volterra predator-prey model with mass-action predation response (Lotka, 1925; Volterra, 1926), described by the system

$$\frac{dx}{dt} = ax - bxy, \quad (1)$$

$$\frac{dy}{dt} = cbxy - dy, \quad (2)$$

where

x : prey biomass density, y : predator biomass density,
 a : prey growth rate, b : per capita predation rate,
 c : biomass conversion efficiency, d : predator death rate.

The interior equilibrium point $(x^*, y^*) = \left(\frac{d}{cb}, \frac{a}{b}\right)$ is neutrally stable (a center), at which the predator:prey biomass ratio is

$$\frac{y^*}{x^*} = \frac{ac}{d}. \quad (3)$$

The ratio is greater than 1 if and only if $ac > d$. We obtain our first result in biomass pyramid theory:

Result 1 *For the model (1)-(2), if $ac > d$ (the prey growth rate multiplied by the conversion efficiency is greater than the predator death rate), the biomass pyramid is inverted; otherwise, the biomass pyramid is standard.*

Result 1 provides a rigorous foundation for the belief expressed by some biologists that inverted biomass pyramids result from the high growth rate of prey and low death rate of predators (Del Giorgia et al., 1999). Result 1 further suggests that the biomass conversion efficiency can significantly influence the shape of the biomass pyramid.

We now incorporate a general well-mixed predation response into the predator-prey model, which is described by the system

$$\frac{dx}{dt} = ax - f(x)y, \quad (4)$$

$$\frac{dy}{dt} = cf(x)y - dy, \quad (5)$$

where

$f(x)$: predation response function.

At the interior equilibrium point (\hat{x}, \hat{y}) , the ratio $\hat{y}/\hat{x} = a/f(\hat{x})$, where $f(\hat{x}) = d/c$. Thus the predator:prey biomass ratio is

$$\frac{\hat{y}}{\hat{x}} = \frac{ac}{d}. \quad (6)$$

This interior equilibrium point is attracting when the system (4)-(5) is eventually bounded and has no stable limit cycles. The system is eventually bounded if there is a bounded region where all solutions eventually enter into and stay in. Result 1 remains valid for this extended model whenever the interior equilibrium point is stable. Actually, whenever the prey grow exponentially, Result 1 is robust to variations in refuge-dependent predation patterns.

We now incorporate logistic prey growth into the preceding predator-prey model, which is described by the system

$$\frac{dx}{dt} = ax \left(1 - \frac{x}{K}\right) - f(x)y, \quad (7)$$

$$\frac{dy}{dt} = cf(x)y - dy, \quad (8)$$

where

K : prey carrying capacity,

and the predation functional response $f(x)$ is a strictly increasing function. Any reasonable predation function must satisfy this monotone condition, which

all three Holling-type functions do. The monotonicity implies that the inverse function f^{-1} exists (Inverse function in Wikipedia, internet), and thus the x -component of the interior equilibrium point can be solved from $cf(x) = d$ as $\tilde{x} = f^{-1}(d/c)$. The biomass ratio at the interior equilibrium point (\tilde{x}, \tilde{y}) can be written as

$$\frac{\tilde{y}}{\tilde{x}} = \frac{ac}{d} \left[1 - \frac{f^{-1}(d/c)}{K} \right]. \quad (9)$$

This formula modifies the biomass ratio in model (1)-(2) and model (4)-(5) by the factor $1 - \frac{f^{-1}(d/c)}{K}$. This interior equilibrium point is attracting when the predator-extinction equilibrium $(K, 0)$ is unstable and there exist no stable limit cycles. For instance, if $f(x) = \frac{bx}{\eta + x}$ is a Holling type II functional response, then the interior equilibrium point is globally attracting whenever $\frac{\eta d}{b-d} < K < \frac{\eta(b+d)}{b-d}$. Under the stability condition, we obtain the new result:

Result 2 *For the model (7)-(8), if $\frac{ac}{d} \left[1 - \frac{f^{-1}(d/c)}{K} \right] > 1$, the biomass pyramid is inverted; otherwise, the biomass pyramid is standard.*

The new condition for the inverted biomass pyramid depends additionally on the prey carrying capacity K . We see that the predator:prey biomass ratio is an increasing function of the prey growth rate (a), the conversion efficiency (c), and the prey carrying capacity (K), while the biomass ratio is a decreasing function of the predator death rate (d). As a conclusion, we have the following result:

Result 3 *The increase of prey growth rate, the conversion efficiency, the prey carrying capacity, or the predator life span facilitates the occurrence of inverted biomass pyramids.*

Result 3 is robust whenever the predation function is an increasing function of prey density. We will see in the next section that the same relations hold for refuge-dependent predation functions.

3 Refuge Mechanism

Seeking refuge from predators is a general behavior of most animals in *natural* ecosystems (Cowlshaw, 1997; Sih, 1997) where the refuge habitats can include burrows (Clarke et al., 1993), trees (Dill and Houtman, 1989), cliff faces (Berger, 1991), thick vegetation (Cassini, 1991), or rock talus (Holmes, 1991). Some ecologists even believe that refuges provide a general mechanism for interpreting ecological patterns (Hawkins et al., 1993), specifically the extent of predator-prey interactions (Huffaker, 1958; Legrand and Barbosa, 2003; Rossi et al., 2006). Aquatic ecologists have recently observed inverted biomass pyramids in pristine coral reefs, where the benthic coral cover provides the refuge for prey fish (Friedlander and Martini, 2002; Sandin et al., 2008).

In Singh et al. (2008), we needed to introduce a refuge with explicit size. Although the Holling type III functional response offers the prey a refuge at low population density (Murdoch and Oaten, 1975), the refuge is only implicit, and one can not specify the size of the refuge. Some authors include an explicit refuge size into their models by multiplying the prey density by $1-r$, where $0 \leq r < 1$ is a proxy of the refuge size (McNair, 1986; Sih, 1987; Hausrath, 1994; Kar, 2005; Huang et al., 2006; Kar, 2006; Ko and Ryu, 2006). This procedure has two fundamental drawbacks. The first is that for these modified predation response functions, the switch point, where the predation rate starts to quickly

increase, critically depends on both the proxy refuge size and the proxy half-saturation constant (independent of the refuge size). The latter dependence is undesirable. For our model, it is important that the switch point be a function of only the refuge size. The second drawback is that, unlike the Holling-type functional responses which are mechanistically derived from basic biological principles, we have seen no derivation in the literature and we are unable to mechanistically derive these functional forms from basic biological principles to incorporate a refuge.

We now introduce a family of predator-prey models with explicit refuge size, which we call **refuge-modulated predator-prey (RPP) models**. An important feature of this family is that the switch points for the functional responses depend solely on the size of the refuge. We group these models into three classes, RPP Types I, II, and III, depending on the mechanistic dependence of prey availability for predators on the refuge size. All previous refuge models assume the mechanism behind our Type I class.

3.1 Refuge-Modulated Predator-Prey Models

In our recent work (Singh et al., 2008), we modeled the biomass of fish in coral reefs. Small fish find refuge in coral reefs by hiding in holes where large predators cannot enter (Hixon and Beets, 1993). This field observation motivated us to incorporate a refuge into the standard predator-prey model, where the coral reef refuge size influences the pattern of predation response. We introduced the following family of models:

$$\frac{dx}{dt} = ax \left(1 - \frac{x}{K}\right) - f(x, r)y, \quad (10)$$

$$\frac{dy}{dt} = cf(x, r)y - dy, \quad (11)$$

where

r : refuge size,

$f(x, r)$: refuge-dependent predation response,

and $f(x, r)$ is a strictly increasing function of prey biomass density x . For each fixed r , the function $f_r(x) = f(r, x)$ is strictly increasing in x , and thus its inverse f_r^{-1} exists. We solve for the x -component of the interior equilibrium point from $cf(x, r) - d = 0$ as $\bar{x} = f_r^{-1}(d/c)$. The biomass ratio at the interior equilibrium point (\bar{x}, \bar{y}) :

$$\frac{\bar{y}}{\bar{x}} = \frac{ac}{d} \left[1 - \frac{f_r^{-1}(d/c)}{K}\right]. \quad (12)$$

For each fixed refuge size r , the relationships between the biomass ratio and other parameters are the same as in the well-mixed predator-prey models. This provides the robustness of Result 3. Additional hypotheses are needed to determine the relationship between the biomass ratio and the refuge size. Although the field observation in Hixon and Beets (1993) suggests that prey fish hide in refuge places from predators, it is still unclear how the refuge regulates the prey availability for predators. In the next subsection, we propose three hypotheses all motivated from biological considerations.

3.2 Hypotheses on Refuge Effects

We model three biological hypotheses on how prey availability for predators depends on the refuge size (Figure 2). We call these models RPP (Refuge-modulated Predator-Prey) Type I, Type II, and RPP Type III. All predation functions depend on the maximum predation rate b , the refuge size r , the minimum predation rate regulator β , and the slope regulator ξ .

RPP Type I: This model assumes that the prey availability for predators decreases as the refuge size increases. Prey hide in the refuge, but trade-off protection (i.e. increased survival) for a decrease in growth or reproduction due to lower quality resources within the refuge (Persson and Eklov, 1995; Gonzalez-Olivares and Ramos-Jiliberto, 2003; Reaney, 2007). Thus an increase in the size of the refuge protects more of the prey and results in less prey available to the predator. Thus, the prey availability for predators is the prey density outside the refuge and $f(x, r)$ is a decreasing function of refuge size r . We choose the following representative function that can be fitted to empirical data:

$$f(x, r) = \frac{b}{1 + \beta e^{-\xi(x-r)}}. \quad (13)$$

The variable x is the total prey density (per unit area) and thus the prey availability for predators is $x - r$.

The parameter β captures the minimum predation rate as follows: when no prey and no refuge are available, the predation rate is $\frac{b}{1 + \beta}$, which is the minimum predation rate. We should choose β sufficiently large such that $\frac{1}{1 + \beta} \ll 1$, since it is reasonable to have a small predation rate when no prey are available. The parameter ξ determines the slope of the predation

curve when x is close to r . The prey density at the interior equilibrium point is $\bar{x} = f_r^{-1}(d/c) = r - \frac{1}{\xi} \ln \left[\frac{1}{\beta} \left(\frac{bc}{d} - 1 \right) \right]$. The interior equilibrium point only exists when $bc > d$. To see this, if $bc \leq d$ and $\beta > 0$, then $\frac{dy}{dt} < (bc - d)y \leq 0$, and thus predators go extinct since all solutions tend to the boundary equilibrium point $(K, 0)$. Biologically, when the maximum predation rate multiplied by the conversion efficiency is less than the predator death rate, one would expect that predators cannot persist. Under the conditions that β is sufficiently large and $bc > d$, the term $\frac{1}{\xi} \ln \left[\frac{1}{\beta} \left(\frac{bc}{d} - 1 \right) \right]$ is negative. Hence,

$$\bar{x} = f_r^{-1}(d/c) = r - \frac{1}{\xi} \ln \left[\frac{1}{\beta} \left(\frac{bc}{d} - 1 \right) \right] = \boxed{r + \frac{1}{\xi} \ln \frac{\beta d}{bc - d} > 0} \text{ for sufficiently large } \beta.$$

The evidence for the presence of trade-offs (survival vs. growth or reproduction) with the use of refuges is plentiful (Lima and Dill, 1990; Persson and Eklov, 1995; Reaney, 2007). However, we are aware of only one experimental example that shows a decrease in growth rate of the predator in response to the use of a refuge by the prey (Persson and Eklov, 1995).

RPP Type II: This model assumes that the prey availability for predators is independent of the refuge size (in the sense of density, per unit area), i.e. $f(x, r)$ is a constant function of r . Prey biomass within the refuge may increase, but the amount available to the predators remains the same. We choose our representative RPP Type II predation function:

$$f(x, r) = \frac{b}{1 + \beta e^{-\xi x}}. \quad (14)$$

The variable x is the prey density, and the parameters b , β , and ξ have the same meanings as in RPP Type I. The x -component of the interior equilibrium

point is $\bar{x} = f_r^{-1}(d/c) = \boxed{\frac{1}{\xi} \ln \frac{\beta d}{bc - d} > 0}$ for $bc > d$ and sufficiently large β .

We know of no biological examples of RPP Type II. However, we believe that RPP Types I and III are the extremes of a continuum, suggesting that condition can exist where the prey available to predators is not affected by the area within the refuge.

RPP Type III: This model assumes that the prey availability for predators increases as the refuge size increases. This may occur when resources such as food and mating sites are available within the refuge, allowing the prey to increase in numbers until some limiting resource forces a number of the prey to emigrate from the refuge in search for new habitat. The number of immigrants should be positively related to refuge size. Thus, $f(x, r)$ is an increasing function of r . Our representative RPP Type III predation function looks quite similar to our Type I predation function, but the parameters require different interpretations:

$$f(x, r) = \frac{b}{1 + \beta e^{-\xi(x+r)}}. \quad (15)$$

The variable x is the exterior (out of refuge) prey density (per unit area), and $x + r$ is the total prey density (per unit area). This model assumes that the refuge stores a substantial amount of prey and constantly provides food to predators, and thus the prey availability is the total prey density (per unit area), i.e. $x + r$.

For $bc > d$ and β sufficiently large such that $\frac{1}{\xi} \ln \frac{\beta d}{bc - d} > 0$, the x -component of the interior equilibrium point is $\bar{x} = f_r^{-1}(d/c) = \boxed{-r + \frac{1}{\xi} \ln \frac{\beta d}{bc - d} > 0}$ for $r < \bar{r}$. The threshold refuge size $\bar{r} = \frac{1}{\xi} \ln \frac{\beta d}{bc - d} > 0$ for $bc > d$ and sufficiently

large β . Because the refuge size in the model is measured by density (per unit area), it is biologically reasonable to assume a threshold maximum value for the refuge size.

The Elk Refuge in Yellowstone National Park is one example of a RPP Type III. The Elk Refuge provides protection (and food) to the elk during winter increasing survival to 97% (Lubow and Smith, 2004). The surviving elk migrate out of the refuge and provide a source of food for predators in Yellowstone National Park and surrounding areas (Smith, pers. comm., 2008). Our RPP Type III is also analogous to spillover and larval export hypotheses in marine protected areas (MPA) (Ward et al., 2001). MPAs are areas of the ocean that are protected from fishing (i.e. man is the predator). The fish within these MPAs are hypothesized to increase the number of fish (prey) available outside the protected area through two mechanisms. The first, spillover, occurs when adult fish become crowded within the MPA and immigrate into the surrounding area. The second occurs when the fish within the MPA increase their reproductive output, increasing the number of recruits available to surrounding areas (larval export). While support for the spillover hypothesis is present (though limited spatially), it is much harder to prove the benefits of larval export (Ward et al., 2001).

We now make a couple of general remarks about the RPP-type functional responses. We always assume that $f(0, r) > 0$ and small, i.e. for each fixed r , the predation rate at zero prey density is positive, but minimal. For Holling-type responses, $f(0, r) = 0$. We believe our choice is reasonable, since when the main prey species are no longer available, predators may temporarily switch to alternative lower quality food sources (Warburton et al., 1998). Thus, one

must choose β sufficiently large such that $\frac{1}{1+\beta} \ll 1$. If we fit this predation function to empirical data, ξ may need to be chosen large, depending on the size of β . When the prey availability is high, $f(x, r)$ is close to the maximum predation rate b . Mathematically, the refuge size r solely determines the shift of the predation curve.

3.3 Dependence of Biomass Ratio on the Refuge Size

In this subsection, we use (12) to analyze the effects of the refuge size on the predator:prey biomass ratio. It is evident that the biomass ratio in (12) is a decreasing function of $f_r^{-1}(d/c)$.

For RPP Type I, the term $f_r^{-1}(d/c) = r + \frac{1}{\xi} \ln \frac{\beta d}{bc - d}$ is an increasing function of the refuge size r . Thus, the predator:prey biomass ratio at the interior equilibrium point is a decreasing function of the refuge size r .

For RPP Type II, the predator:prey biomass ratio is independent of the refuge size.

For RPP Type III, the term $f_r^{-1}(d/c) = -r + \frac{1}{\xi} \ln \frac{\beta d}{bc - d}$, is decreasing as the refuge size r increases. Thus, the predator:prey biomass ratio at the interior equilibrium point is an increasing function of the refuge size r .

The following results immediately follow from these observations:

Result 4 *For the model (10)-(11), if $\frac{ac}{d} \left[1 - \frac{f_r^{-1}(d/c)}{K} \right] > 1$, the biomass pyramid is inverted; otherwise, the biomass pyramid is standard.*

Result 5 *For RPP Type I, the decrease of the refuge size facilitates the occurrence of inverted biomass pyramids. For RPP Type II, the refuge size has no effects on biomass pyramids. For RPP Type III, the increase of the refuge size facilitates the occurrence of inverted biomass pyramids.*

As an illustrative example, data from Kingman and Palmyra (Sandin et al., 2008) suggests that the predator-prey biomass ratio is an increasing function of the refuge size (equivalent to the benthic coral cover), and thus the appropriate predation response function is RPP Type III. RPP Type III may be biologically appropriate if increases in refuge size either increase recruitment or increase the survival of recruits (Shulman, 1984; Doherty and Sale, 1985). After the surviving recruits grow into juveniles or adults, they leave the refuge and provide an increase in the food available to the predators.

4 Immigration Mechanism

Reef ecologists observed significant immigration of prey fish in a North Carolina reef (M. Hay, pers. comm., 2008). We consider two types of immigration: (i) immigrating prey fish stay in the coral reef and adapt to survive in the new habitat; (ii) immigrating prey fish leave the coral reef if they are not eaten by hungry predators, i.e. they provide additional food to predators but do not add to the local prey population. In this section, we incorporate both types of immigration into the Lotka-Volterra predator-prey model:

(i)

$$\frac{dx}{dt} = ax - bxy + \iota, \quad (16)$$

$$\frac{dy}{dt} = cby - dy; \quad (17)$$

(ii)

$$\frac{dx}{dt} = ax - bxy, \quad (18)$$

$$\frac{dy}{dt} = cb(x + \iota)y - dy; \quad (19)$$

where ι is the constant immigration rate. For case (i), the predator:prey biomass ratio at the interior equilibrium point (\tilde{x}, \tilde{y}) is

$$\frac{\tilde{y}}{\tilde{x}} = \frac{ac}{d} + \iota \frac{c^2b}{d^2}. \quad (20)$$

For case (ii), the predator:prey biomass ratio at the interior equilibrium point (\hat{x}, \hat{y}) is

$$\frac{\hat{y}}{\hat{x}} = \frac{ac}{d - \iota cb}. \quad (21)$$

In both immigration cases, the biomass ratios are increasing functions of the immigration rate ι . This remains true when we incorporate these two immigration effects into Holling type or RPP type models. As a conclusion, we obtain the following robust result:

Result 6 *The immigration of prey facilitates the occurrence of inverted biomass pyramids.*

5 Discussion

We develop a theory of biomass pyramids. Our major contributions can be summarized as follows. First, when prey grow exponentially, the biomass pyramid is inverted if and only if the prey growth rate multiplied by the conversion

efficiency is greater than the predator death rate. Second, the increase of prey growth rate, the conversion efficiency, the prey carrying capacity, or the predator life span robustly facilitates the development of inverted biomass pyramids. Third, based on plausible biological hypotheses, we introduce a new series of predator-prey models (called RPP type models) which explicitly and naturally incorporates a prey refuge. Fourth, depending on the nature of an ecosystem, the occurrence of inverted biomass pyramids can be positively or negatively related to, or independent of, the refuge size. Fifth, the immigration of prey facilitates the occurrence of inverted biomass pyramids.

We propose three new refuge-dependent predation functions with explicit refuge size, which capture the three essential biological hypotheses on the refuge (Figure 2). The three can be combined into one function

$$f(x, r) = \frac{b}{1 + \beta e^{-\xi[x-(2-i)r]}}, \quad (22)$$

where i is the index of RPP type, that is, $i = 1$ for RPP Type I, $i = 2$ for RPP Type II, and $i = 3$ for RPP Type III.

Some, but not all, of the prey that hide in the refuge are available to predators. Thus, there should be a discount rate for the refuge size in the predation function of either RPP Type I (assume no prey in the refuge are available) or RPP Type III (assume all prey in the refuge are available). We incorporate this discount rate into the general refuge-dependent predation function:

$$f(x, r) = \frac{b}{1 + \beta e^{-\xi(x+\eta r)}}, \quad (23)$$

where $-1 \leq \eta \leq 1$. This model is close to RPP Type I if $-1 \leq \eta < 0$, close to RPP Type II if $\eta = 0$, and close to RPP Type III if $0 < \eta \leq 1$. We call η as the refuge-effect parameter.

What characteristics of the prey might lead to RPP Type I versus RPP Type III? As stated above, RPP Type I will occur when the use of the refuge results in strong trade-offs between survival and reproduction or growth. Most previous theoretical models assume that the hypothesis for RPP Type I is the case; however, we hypothesize that RPP Type III will occur when the prey have the ability to reproduce within the refuge and/or when the refuge increases prey survival through a population bottleneck.

Prey animals seek refuges to hide from predators and thus it is sometimes necessary to explicitly incorporate the refuge mechanism into the predation function of predator-prey models. The family of RPP-type models explicitly incorporating the refuge size can more accurately describe realistic predator-prey interactions in ecosystems. We believe that RPP-type models provide the next generation of models for predator-prey interactions. In the coming Winter, we plan to test these models via microcosm experiments.

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Figure 1. This figure is reproduced from Sandin et al. (2008). At Kingman coral reef, it was recently discovered that apex predators constitute 85% of the total fish biomass. The biomass pyramid is clearly inverted in this pristine coral reef. This is in sharp contrast to most reefs where the prey biomass substantially dominates the total fish biomass.

Figure 2. Three biological hypotheses for the effects of the refuge size on the prey availability for predators. Type I: the prey availability for predators is a decreasing function of the refuge size, because the refuge provides places for prey to hide from predators. Type II: the prey availability for predators is independent of the refuge size in the sense of density (per unit area), because in a number of cases prey biomass is proportional to the refuge size. Type III: the prey availability for predators is an increasing function of the refuge size, because the refuge both provides prey to predators and stores prey for latter consumption by predators.



Fig. 1. The pristine coral reef at Kingman.

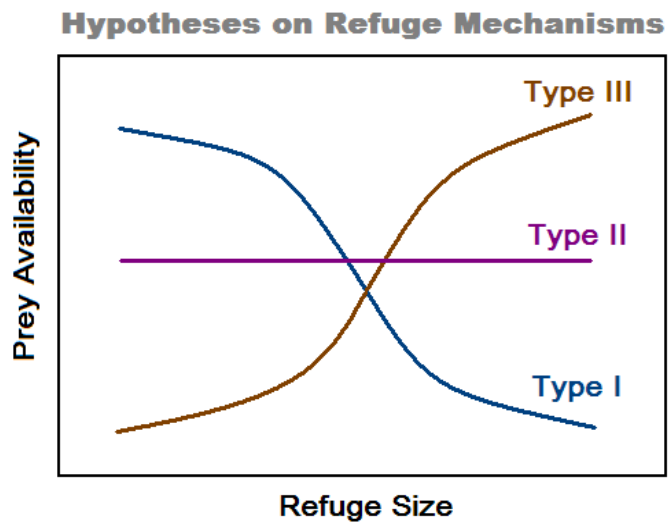


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